Observations on the Nesting Behavior of *Crossocerus* (*C.*) *maculiclypeus* (Fox) (Hymenoptera: Sphecidae)

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Received for Publication February 20, 1969

Abstract: Studies on the nesting behavior of seven females of *Crossocerus maculiclypeus* in an aggregation of several hundred individuals are detailed. The wasps apparently selected pre-existing burrows in sand for use as nest sites. A female carried her prey directly into the open nest. Burrows leading to fully provisioned cells were partly filled with loose sand.

The nests varied considerably in form and dimensions. The maximum number of cells per completed nest appeared to be nine; other finished nests contained from four to six cells. The small cells were constructed in clusters which were often separated by several centimeters. Fully provisioned cells contained from 9 to 20 paralyzed or dead flies. The empidid *Platypalpus holosericus* was the dominant kind of prey; other species of Empididae, Dolichopodidae, and Agromyzidae were less commonly stored. Single species each of Psilidae, Tephritidae, and Chamaemyiidae were also used as provisions. More flies were stored ventral side up, head inward than in any other position. The wasp's egg was attached by the cephalic end to the ventral side of the neck of one of these flies in each cell.

The genus *Crossocerus* contains 9 subgenera and about 40 species in the United States and Canada (Krombein, *in* Muesebeck, *et al.*, 1951; Krombein, 1958b; Krombein and Burks, 1967). Relatively little is known about the nesting behaviors of the Nearctic species. Species in the subgenera *Ablepharipus, Blepharipus, Stictoptila,* and *Epicrossocerus* nest in rotten logs, twigs and stems, and various other plant materials, frequently utilizing the abandoned burrows of small wood-boring beetles [Hamm and Richards, 1926; Davidson and Landis, 1938; Erikson, 1940; Pate, 1944 (1943); Steyskal, 1944; Krombein, *in* Muesebeck, *et al.,* 1951; Krombein, 1958a, 1958b, 1964; Krombein and Burks, 1967]. The majority of species in these subgenera provision their nest cells with small adult Diptera. As Pate [1944 (1943)] pointed out, females of species which nest in plant materials are characterized by a narrow pygidium with an apical excavation. Although lacking this structural adaptation, females of *Crossocerus* (*C.*) *planifemur* Krombein also nest in tunnels in logs (Krombein, 1952, 1958b). Other species in this subgenus exhibit similar nesting habits [Pate, 1944 (1943)]. The majority of species in *Crossocerus s. str.*, however, as well as species in the subgenera *Hoplocrabro, Microcrabro, Synorhopalum,* and

Acknowledgments: We are indebted to K. V. Krombein and A. S. Menke, Smithsonian Institution and U. S. National Museum, for identifying the wasps; and to their associates, L. V. Knutson and G. Steyskal for determining the prey flies. (The wasps and flies have been deposited in the collection of the U. S. National Museum and bear ethology note no. labels CS-1 through CS-8).

probably *Yuchiha* nest in sandy or clay soils and stock their cells mostly with small adult Diptera [Cockerell, 1898; Peckham and Peckham, 1905; Smith, 1908; Rau, 1922; Hamm and Richards, 1926; Pate, 1944 (1943); Krombein, 1963]. Females of these species possess a broad, flat, trigonal, rather coarsely punctate pygidium [Pate, 1944 (1943)]; thus the shape of the female pygidium appears to be a good indicator of nesting habits in this genus. Virtually nothing is known about the nesting behavior of the single Nearctic species in the subgenus *Nothocrabro, nitidiventris* (Fox). Using Pate's [1944 (1943)] criterion of the shape of the female pygidium for determining nesting habits, members of this subgenus would be expected to nest in plant materials.

Among the ground-nesting species, the European *C.* (*Hoplocrabro*) *quadrimaculatus* (Fabr.) nests in sand and stocks its cells with nematocerous and brachycerous Diptera and Trichoptera (Krombein, *in* Muesebeck, *et al.*, 1951; Grandi, 1961). Females of *C. scutellatus* Say [= *C.* (*Yuchiha*) *xanthochilos* Pate] were observed by Rau (1922) entering holes in a clay bank in Kansas. He was unable to ascertain whether the wasps were foraging or nesting in the holes. Pate [1944 (1943)], observing soil particles on the legs of species of *Yuchiha*, surmised that they nested in the ground. *C.* (*Synorhopalum*) *decorus* (Fox) was observed nesting in the ground by both Cockerell (1898) and Smith (1908), but they presented little information on its nesting behavior.

Hamm and Richards (1926) reviewed the nesting behaviors of six species of European *Crossocerus s. str.* (*palmarius* Schreb., *palmipes* L., *varius* Lep., *anxius* Wesm., *wesmaeli* V. de Lind., *elongatus* V. de Lind.) and presented their own observations on five of the species. The wasps nested mostly in the ground, frequenting sandy soils, often banks. Colonies were indicated by numerous small tumuli surrounding the nest entrances. Females of *C. palmipes*, returning with prey, flew straight into their nests without hesitating. The nests of all species were rather short and shallow, and, depending on the species, either uni- or multicellular. Some tunnels of *C. varius* entered the ground obliquely, but coursed perpendicularly a few centimeters beneath the surface. The number of prey stored per cell in this species ranged from 7 to 14. As many as six or seven species were stored in a single cell. The kinds of prey varied with different species of wasps. Some species (*palmarius, palmipes, elongatus, wesmaeli, varius*) preyed only on small, often nematocerous Diptera. Other species, such as *C. anxius*, stored both Diptera and Hemiptera.

Crossocerus (*C.*) *lentus* (Fox) was observed by Peckham and Peckham (1905) nesting in the ground. One nest went obliquely downward for 6.5 cm, terminating in a cell. The incompletely provisioned cell contained "two bugs and a fly." Rau (1922) noted a female of *Crossocerus incavus* Fox [= *C.* (*C.*) *planipes* (Fox)] entering a hole in a clay bank, and later "kicking" loose dirt out of the entrance. Possibly, the wasp was renovating this hole for use as a nest site.

FIG. 1. Nesting site of *Crossocerus maculiclypeus* near Chittenango, Madison County, New York.

Krombein (1963) has presented the most detailed observations on the nesting habits of Nearctic species of *Crossocerus s. str.* He studied the nests of two females of *Crossocerus* (*C.*) *planipes* in Maryland. Both nests occupied partly shaded bare soil. One nest plunged downward at an angle of 20°–30° to the surface, bending abruptly twice, and ending in a cell, 3 cm beneath the surface. The incompletely stocked cell contained two small empidid flies of the genus *Drapetis*. A second cell in this nest, 2 cm beneath the surface, held 16 flies of the same species, of which one bore the wasp egg. Both cells were 6 mm long and ovoid in shape. In the second nest excavated by Krombein (1963) the entrance, 3 mm in diameter, was surrounded by a tumulus of sand, 15 mm wide and 25 mm long. The burrow proceeded downward at a "shallow" angle for 3 cm to a depth of about 1 cm beneath the surface, turned downward at a 60° angle to the horizon, and ended 2 cm below the surface. A cell, 2 cm from this burrow, was unearthed 2.5 cm beneath the surface. It contained 13 paralyzed, small empidids of the genus *Chersodromia*. Krombein (1963) believed that he lost the wasp egg upon removing the flies from the cell.

Our studies of *Crossocerus* (*C.*) *maculiclypeus* (Fox), a species which inhabits the northern United States and Canada, were made in a sand pit, 1 mile north of Chittenango and 7 miles west of Canastota, Madison County, New York (Fig. 1), during 3–10 June 1968. A second growth stand of mixed hardwoods, mostly oaks, and scattered white pines bordered the northern rim of the pit; the southern edge was bounded by a field. Females always nested in bare hard-packed sand, preferring slopes and ridges to flat sand. Although there were literally hundreds of nesting females, individual nests were usually spaced several centimeters apart, i.e., the wasps were not highly gregarious. Twelve nests occupied one area of about 1 square meter.

Females were not seen constructing their own burrows. The wasps were observed flying from hole to hole, entering and then exiting in flight a few seconds later. Such holes appeared to have been made by bees or other small wasps. Since females of *C. maculiclypeus* lack a foretarsal pecten (Fig. 2), we suspect that they do not construct their own burrows entirely; instead, they probably renovate the abandoned nests of other small insects, primarily hymenopterans.

One female (CS-1)[1] backed out of a small burrow, briefly removed sand from the entrance with the forelegs, flew away, and then entered three other holes nearby in rapid succession. She did not remove sand from any of the three holes. Flying in a zig-zag pattern, she entered three more holes, but abandoned each one. Upon entering an eighth hole, she emerged head first, pushing out sand, apparently using the forelegs and head. Shortly thereafter, she abandoned this burrow. Later, this wasp or another was seen backing out of an entrance to a small burrow, pushing sand backward with the legs and abdomen. A small tumulus of damp sand began forming in and around the entrance. It was not known whether this female had started to dig from the sand surface or had renovated a pre-existing burrow. Once a burrow was completed and provisioning begun, a wasp occupied the site for a period of several days, unless accidentally prevented from doing so. Two wasps (CS-4, 7) were observed provisioning their nests for at least three and four days, respectively, and probably had maintained these sites for even longer periods of time.

Several females, including CS-1, 3, 4, were observed holding their prey beneath the body and darting directly into open holes. Upon close inspection, it appeared that the wasp held the prey with the middle and hind legs. The fly was clasped tightly, ventral side up and head forward, against the ventral surface of the wasp's thorax. Females with prey flew to their nests in a zig-zag manner, many centimeters above the ground. One female (CS-3) took from 3 to 21 (mean, 11; N = 4) minutes between consecutive returns to the nest with prey. After three separate entries, this wasp stayed below the ground 10, 8, and 7 minutes, before exiting to search for the next prey. It was not determined why she spent such long periods of time inside the nest.

Females of *C. maculiclypeus* were not observed filling their burrows with sand after stocking a cell and ovipositing. However, as mentioned, partly filled

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[1] Wasps and prey were given ethological note numbers to facilitate associating individual females and the contents of their nests.

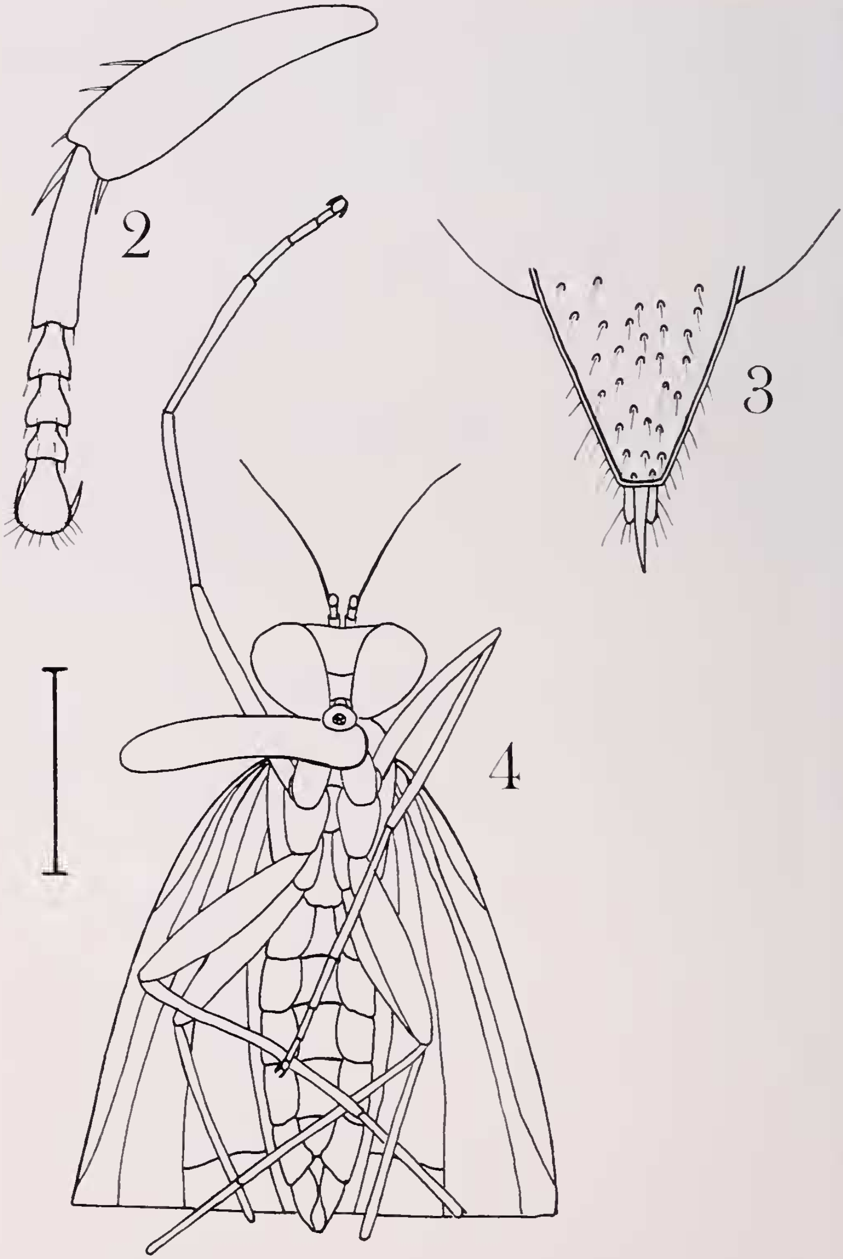


FIG. 2. Foretarsus and tibia of female of *Crossocerus maculiclypeus*.

FIG. 3. Pygidium of female of *Crossocerus maculiclypeus*.

FIG. 4. Egg of *Crossocerus maculiclypeus* in typical position on ventral side of neck of prey dolichopodid. (Scale at left equals 1 mm).

burrows led to completely provisioned cells. Open burrows terminated in incompletely provisioned cells. We believe that the female fills the burrow by packing in sand with the pygidium, either before or during the construction of a new side burrow and cell. The fact that females of *Crossocerus maculiclypeus* have a broad, flat, trigonal pygidium (Fig. 3) suggests this behavior.

We excavated and studied eight nests of *Crossocerus* (*C.*) *maculiclypeus* (CS-1 through CS-8). The nest entrances were 2–3 mm in diameter, suggesting that, if the wasps use pre-existing burrows, they are highly selective of the diameter of the tunnels in which they nest. Entrances to active nests were surrounded by tumuli, each measuring about 2.5 cm in diameter and 1 cm high. The tumuli remain intact until rainfall or an accidental disturbance obliterates them. With the construction of an additional cell, the form and dimensions of a tumulus changed slightly as sand from the new digging was brought to the surface. Only one nest (CS-6) was built in flat sand. The other seven nests were constructed into sand slopes and cliffs. The main burrows, about 2 mm in diameter, entered the sand at angles varying from about 30° (CS-6) to nearly 75° (CS-4) to the surface.

Burrows varied considerably in form and dimensions (Fig. 5). Some, such as CS-1, were rather straight. Others, for example, CS-6 and 8, curved gradually. Another burrow (CS-4) was ∪-shaped at its proximal end. Traceable burrows ranged from 5.5 (CS-1) to 11.5 (CS-4) (mean, 7.2; $N = 6$) cm in length. Such variation in the form and dimensions of these burrows further suggests the use of pre-existing insect burrows as nest sites by females of *C. maculiclypeus*. Some burrows (CS-1, 5) were entirely open or nearly so. Others (CS-2, 4, 6, 8) were filled with sand for much of their lengths, but open for a few centimeters near the entrances. Burrows filled with sand invariably led to completed cells, i.e., cells stocked with prey and a wasp egg or larva. Open burrows terminated in incompletely provisioned cells. Burrows leading to the oldest cells could not be traced with certainty. They are indicated by dotted lines in Fig. 5. These cells often contained mature larvae or cocoons.

Nests such as CS-1, 5, each with 2 cells, were undoubtedly unfinished (Fig. 5). Other nests (CS-2, 4, 6, 8), with closed burrows, were apparently completed. These nests contained 5, 6, 6, and 4 fully provisioned cells, respectively. In another area (CS-7), 14 cells were unearthed. Due to the bimodal distribution in the depths of these cells, we suspect that two nests were involved, one (CS-7a) with 5 cells, the other (CS-7b) with 9 cells. As in other species of crabronine wasps (see Hamm and Richards, 1926; Evans, 1960; Kurczewski and Acciavatti, 1968), nest cells of *C. maculiclypeus* were constructed in rather loose clusters (see, for example, CS-4, 6 in Fig. 5). Clusters of cells in a nest were often separated by several centimeters. Cells in a cluster were connected to side burrows which probably led to a main burrow, but this was impossible to confirm in older nests. Some cells (CS-2A, B, 4C, D, E, 6B, C, D, E, 8B, C, D)

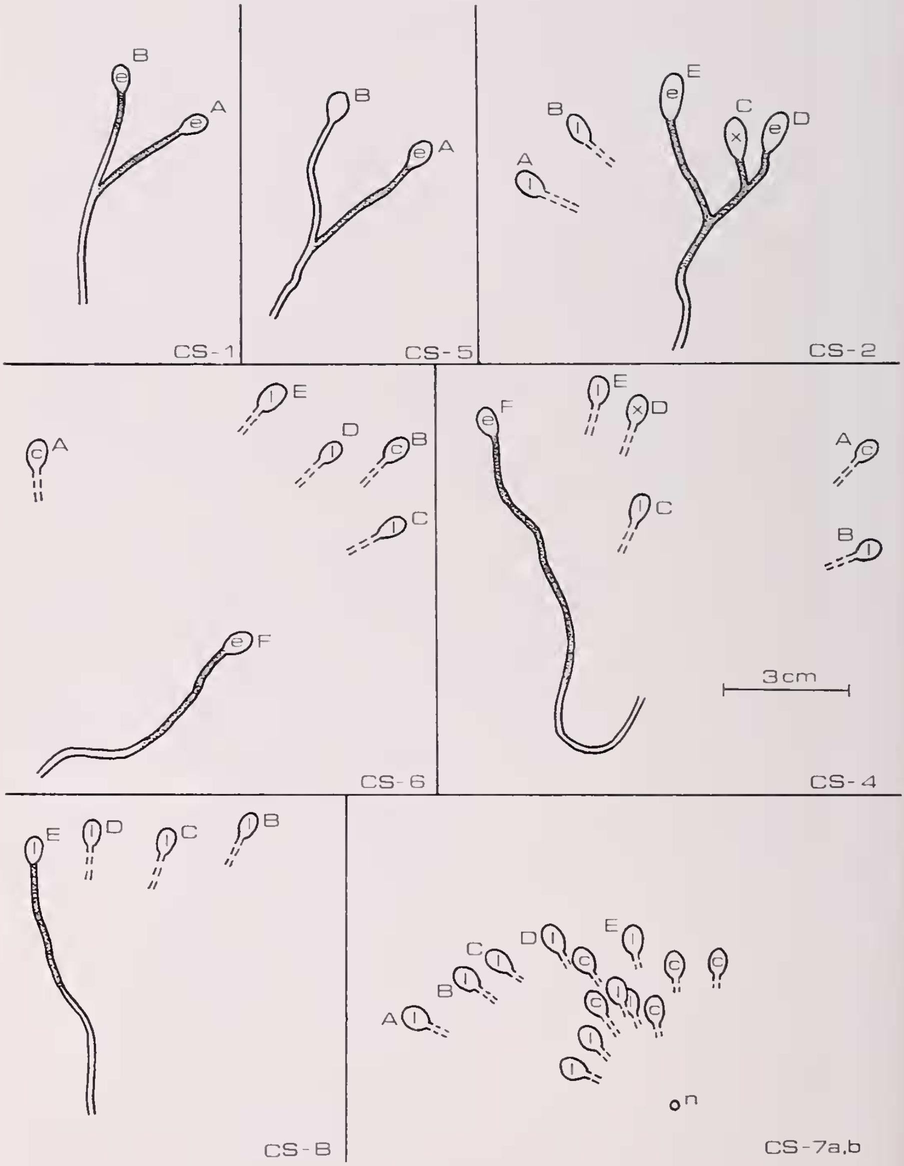


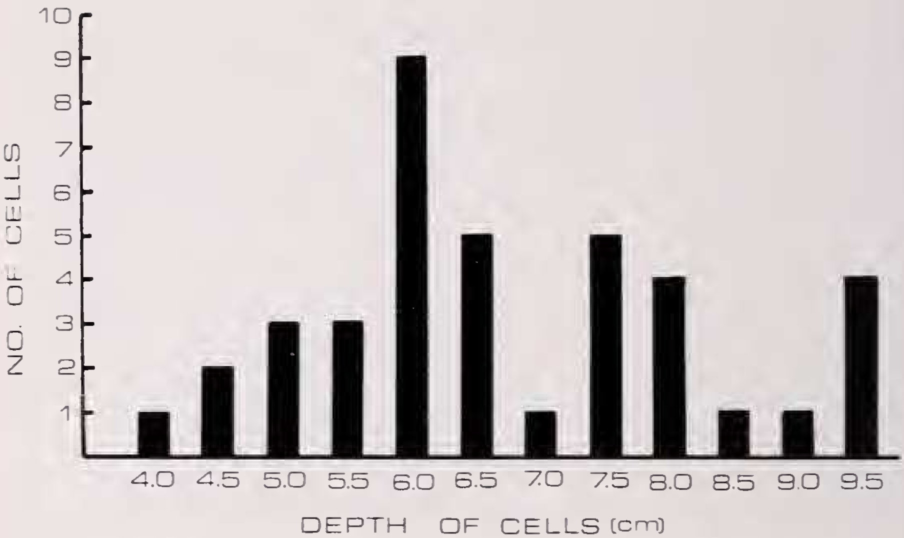
FIG. 5. Burrow and cell configurations in nests of *Crossocerus maculiclypeus*. Dotted lines indicate untraceable burrows. Burrows filled with sand are stippled. Cells are labelled with capital letters, A indicating the probable first cell made, B the second, and so on. Cell contents are as follows: e, egg, l, larva, c, cocoon, x, contents destroyed by mold or parasite; empty cell was incompletely provisioned. The entrance to nest CS-7b is indicated by n.

were unearthed several centimeters from the main burrows with which they were probably associated. Nests CS-1, 2 (cells C, D, E), and 5 indicate the structural configurations of the main burrow, side burrow(s), and associated cells. We did not find prey storage chambers in any of the nests, although we could have easily overlooked them because of the narrow confines of the burrows and the small sizes of the cells and prey. Open burrows are frequently used as storage chambers by other crabronine wasps (see Evans, 1960; Kurczewski and Acciavatti, 1968).

In species of *Crabro*, the first cells made and provisioned in a cluster are often farther from the entrance than cells made and provisioned later (Hamm and Richards, 1926; Evans, 1960; Kurczewski and Acciavatti, 1968). We were unable to clearly demonstrate this in nests of *Crossocerus maculiclypeus*, using as criteria the stages of development of the wasps in the cells and the weights of the larvae. In three nests (CS-2, 4, 6), however, older cells contained cocoons and mature larvae and were built farther from the main burrow than newer cells which contained juvenile larvae and eggs. In nest CS-7a, cells A–E showed a similar correlation. Cells D, E, nearest the entrance, contained juvenile larvae; cell C, third nearest the entrance, an older larva; and cells A, B, farthest from the entrance, nearly mature larvae ready to spin cocoons.

Nest cells of *C. maculiclypeus* were slanted downward in the sand, with the back end slightly deeper than the front. Twenty-seven cells averaged 4.3 (3–5) mm high, 4.8 (3–7) mm wide, and 6.4 (4–9) mm long. Thirty-nine cells varied in depth from 4.0 to 9.5 (mean, 6.7) cm beneath the sand surface (Fig. 6). Cells of nests CS-1, 4, and 5 were exposed at depths of only 4.0–6.5 cm, whereas cells of other nests (CS-6, 7b) were deeper, mostly 7.5–9.5 cm beneath the surface. In one area, as mentioned earlier, two nests were apparently involved, nest 7a with cells, 4.5–6.0 cm deep, and nest 7b with cells, 7–9 cm deep. Cells belonging to a single cluster were exposed at about the same depth.

Females of *Crossocerus maculiclypeus* preyed exclusively on adult flies. The majority of records were for the empidid *Platypalpus holosericus*; other species of Empididae, Agromyzidae, and Dolichopodidae were less commonly used (Table I). Single species each of Psilidae, Tephritidae, and Chamaemyiidae were also stored. Three or more species of flies were found in only 6 of the 22 cells which contained identifiable specimens. Each of only 7 of 22 cells contained two or more families of prey: CS-1B (Empididae, Dolichopodidae); CS-4A (Empididae, Agromyzidae); CS-4C (Empididae, Dolichopodidae, Agromyzidae); CS-4D (Empididae, Agromyzidae, Psilidae); CS-4E (Empididae, Agromyzidae, Tephritidae, Chamaemyiidae); CS-4F (Empididae, Dolichopodidae, Agromyzidae); and CS-5A (Dolichopodidae, Agromyzidae). However, even in these cells there was a decided preference for a particular family of prey, e.g., cells CS-4A, C, D, E, F, and 5A contained mostly agromyzids, cell CS-1B, mostly empidids. In the other 15 cells a single species of prey was almost always stored.



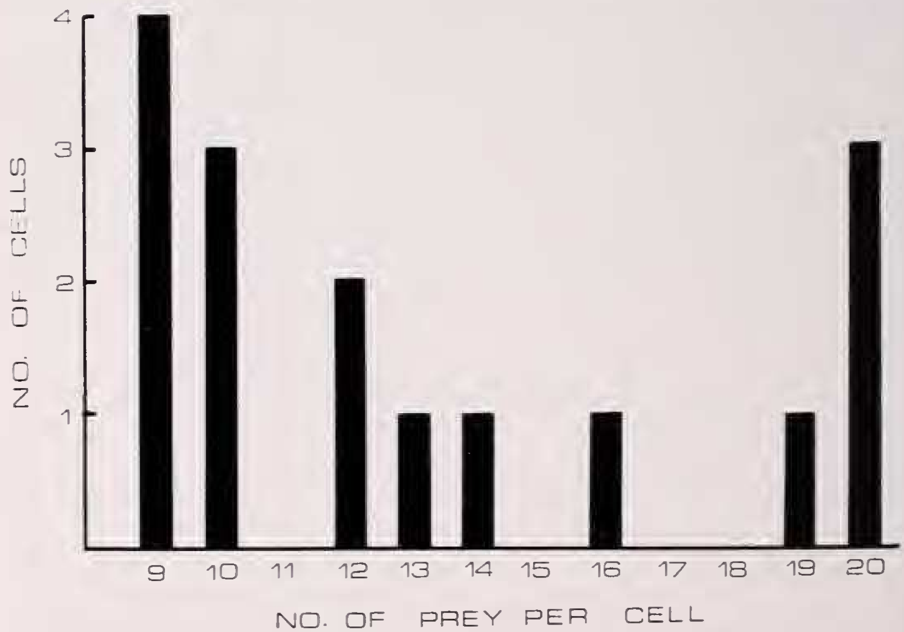


FIG. 6 (ABOVE). Depth of cells in nests of *Crossocerus maculiclypeus*.

FIG. 7 (BELOW). Number of prey per cell in nests of *Crossocerus maculiclypeus*.

TABLE I. Species of Prey of *Crossocerus maculiclypeus*

Family and species of prey	No. of individuals (cells)
Empididae	
Hilara femorata Loew	1♀ (CS-2C)
Platypalpus holosericus Melander	1♀ (CS-1); 8♀ (CS-1A); 6♀ (CS-1B); 11♀ (CS-2A); 9♀ (CS-2B); 13♀ (CS-2C); 6♀ (CS-2D); 5♀ (CS-2E); 9♀ (CS-3A); 3♀ (CS-4A); 1♀ (CS-4C); 1♀ (CS-4D); 1♀ (CS-4E); 1♀ (CS-4F); 4♀ (CS-6C); 2♀ (CS-6D); 7♀ (CS-6B); 8♀ (CS-6F); 9♀ (CS-7G); 9♀ (CS-7K); 6♀ (CS-7L);
Rhamphomyia sp.	1♀ (CS-1A); 2♂ (CS-1B); 1♂ (CS-4A); 1♂ (CS-4C)
Dolichopodidae	
Thrypticus sp.	1♀ (CS-1B); 1♀ (CS-4C); 1 (CS-5A)
Thrypticus willistoni (Wheeler)	1 (CS-4F)
Agromyzidae	
Liriomyza sp.	2 (CS-4D)
Melanagromyza spp.	5 (CS-4A); 5 (CS-4C); 11 (CS-4D); 13 (CS-4E); 14 (CS-4F)
Ophiomyia labiatarum Hering	9 (CS-5A)
Ophiomyia sp.	9♀ (CS-5D)
Phytobia sp.	1 (CS-4C)
Phytomyza sp.	1♀ (CS-4C); 1♀ (CS-5D)
Psilidae	
Psila angustata Cresson	1 (CS-4D)
Tephritidae	
Rhagoletis fausta (Osten Sacken)	1 (CS-4E)
Chamaemyiidae	
Plunomia elegans Curran	1 (CS-4E)

In 14 of these cells the empidid *Platypalpus holosericus* was nearly always or exclusively stored, and *Ophiomyia* sp. (Agromyzidae) in the other cell.

Individual females were very selective of the families and sexes of the flies on which they preyed. Some females showed a decided preference for females of *P. holosericus*—CS-1, 79%; CS-2, 98%; CS-3, 6, 7, 100% (N = 118 specimens). Females CS-4, 5, on the other hand, stored mostly agromyzids of the genera *Ophiomyia* and *Melanagromyza*—CS-4, 73%; CS-5, 90% (N = 86 specimens). The selection of certain sexes and families of prey by some females may reflect the different sizes of the wasps rather than differences in their hunting behaviors. Larger females (CS-2, 6) preferred females of *P. holosericus* and stored fewer, larger individuals per cell, whereas smaller wasps, such as CS-4, captured mostly small agromyzids and stored more flies per cell.

The number of flies stored in fully provisioned cells of *Crossocerus maculiclypeus* ranged from 9 to 20 (mean, 13.3; N = 16) (Fig. 7). The number of prey per cell could not be correlated with either the depth of cell or the distance of cell from entrance or main burrow, i.e., its relative position in the cluster. The

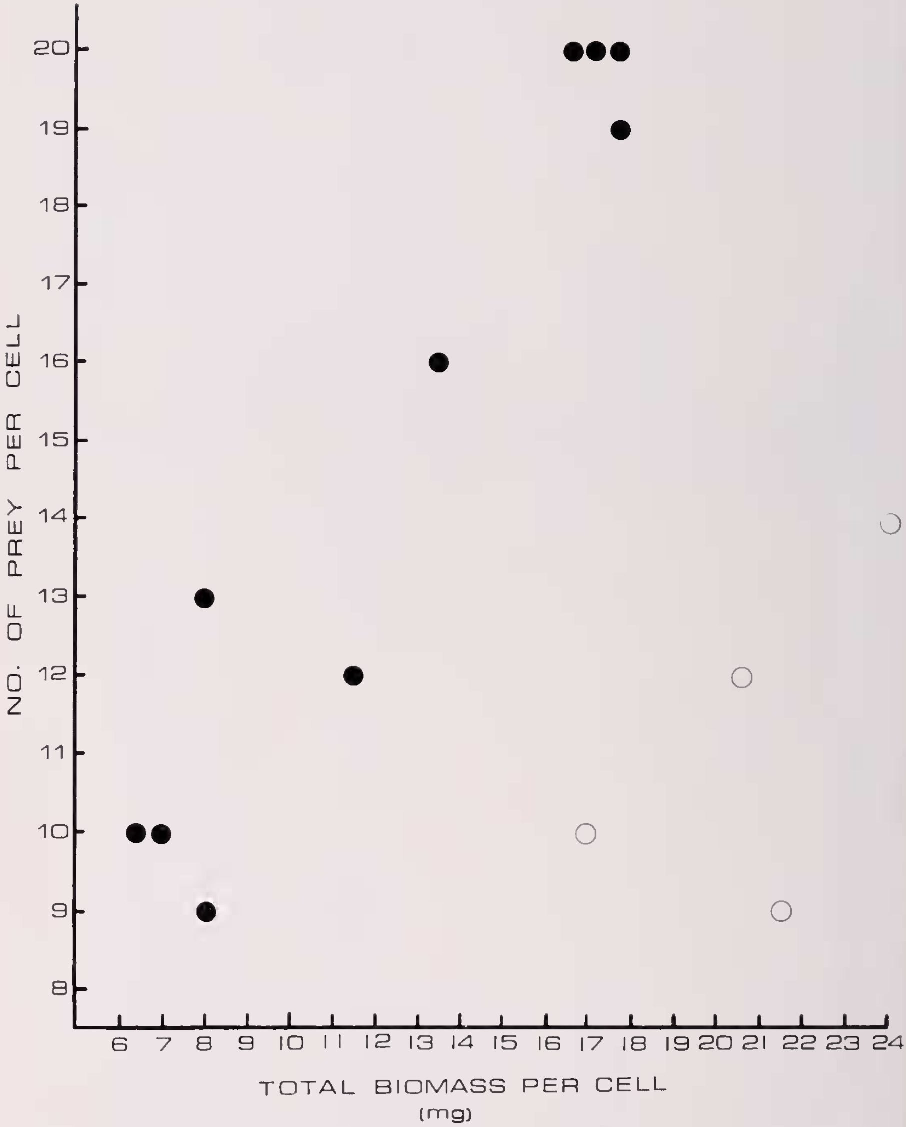


Fig. 8. Total biomass of prey per cell in *Crossocerus maculiclypeus* plotted against the number of prey per cell. (Open circles represent large females, weighing 3.5 mg, and closed circles, small females, weighing 2.5 mg.

weights of the prey individuals ranged from 0.5 to 3.5 (mean, 1.1; N = 206) mg. Larger females, such as CS-2, 6, averaging 3.5 mg in weight, stored larger flies and smaller females, for example, CS-4, weighing 2.5 mg, smaller flies. Thirty-five prey of larger wasps averaged 1.8 mg; 171 prey of smaller wasps, 1.0 mg.

Table II. Position of prey individuals in cells of *Crossocerus maculiclypeus*

Position of prey	No. of individuals
Ventral side up, head inward	64
Ventral side up, head outward	22
Dorsal side up, head inward	29
Dorsal side up, head outward	15
On side, head inward	18
Sideways, head right	10
Sideways, head left	7
Head downward, abdomen upward	4

The total biomass of prey in single cells ranged from 6.5 to 24.0 (mean, 14.7; N = 14) mg. Cells with a greater biomass usually contained more flies, except where larger females had stored larger flies (Fig. 8). An increase in the number of prey per cell did not accompany an increase in cell size.

In 11 of 14 fully provisioned cells, more flies were placed ventral side up, head inward than in any other position. One cell had the majority of individuals placed on their sides and head inward; in two cells, prey were positioned mostly dorsal side up, head outward or ventral side up, head outward. The positions in which 169 prey individuals in 14 fully provisioned cells were placed are summarized in Table II.

In most cases the egg-bearing flies, always one in each cell, were found at the bottom of the cell, either near the middle or at the back end. In 8 of 9 examples, the fly on which the wasp had laid her egg was placed ventral side up and head inward. One egg-bearer was positioned ventral side up, head outward. Egg-bearing prey were average-sized individuals. The egg was never laid on a fly that was conspicuously larger or smaller than other flies in the cell. Eggs were attached to the left or right sides of the prey in about equal numbers.

Eggs of *C. maculiclypeus* were white in color, elastic, cylindrical, curved, elongate, and, after being placed in 70% alcohol for 48 hours, measured about 1.2–1.5 mm long and 0.35–0.45 mm wide. An egg was affixed by the cephalic end to the ventral side of the neck of the fly (Fig. 4). The caudal end extended free to one side in a lateral direction.

Development and behavior of the immature stages of *Crossocerus maculiclypeus* were not studied. Since our studies were made only in early June we were unable to determine whether or not this species is multivoltine at this latitude.

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